

# Role of aphid predator guild in controlling spirea aphid populations on apple in West Virginia, USA

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## Abstract

Spirea aphid populations and their predators were studied on apple to identify predators of importance in controlling aphid populations. Methods included random and non-random sampling from apple orchards in West Virginia, USA, sentinel aphid colonies, laboratory feeding studies, and predator exclusion studies. *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae), chrysopids (Neuroptera: Chrysopidae), *Harmonia axyridis* (Coleoptera: Coccinellidae), and *Orius insidiosus* (Hemiptera: Anthrenidae) were the most abundant predators associated with spirea aphid colonies on apple. Parasitoids were all but absent in the study. Abundance of all predators was density dependent with greater responses to aphid populations at the orchard scale than to tree or individual colony scales. *A. aphidimyza*, *O. insidiosus*, chrysopids, and syrphids (Diptera) had the greatest degree of density dependence on aphid populations, and spiders showed inverse density dependence. Exclusion of predators with both cages and insecticides produced significantly higher aphid populations. Because of high abundance, good synchrony with aphid populations, and high impact per individual, *H. axyridis* adults were the most important spirea aphid predator on apple. Published by Elsevier Inc.

**Keywords:** *Malus domestica*; *Aphis spiraeicola*; *Harmonia axyridis*; *Aphidoletes aphidimyza*; Biological control; Predator impact

## 1. Introduction

Spirea aphid, *Aphis spiraeicola* Patch, and apple aphid, *Aphis pomi* DeGeer, are common pests of apple throughout much of the world (Blackman and Eastop, 1984). In eastern North America, there has been a relatively recent shift from apple aphid to spirea aphid as the most common aphid on apple (Pfeiffer et al., 1989) as a result of competitive displacement (Brown et al., 1995). Apple aphid and spirea aphid are very similar in their ecology on apple (Brown et al., 1995) and their effects on the apple tree (Kaakeh et al., 1993). *Aphis* spp. can cause direct damage to apple fruit in high population densities by feeding on the fruit (Oatman and Legner, 1961), but in most cases the damage is indirect through reductions in general vigor of the apple tree (Hamilton et al., 1986). Kaakeh et al. (1992) showed a

reduction in the amount of photosynthate produced by aphid-infested leaves. Spirea and apple aphids are important indirect pests of apple in North America that require monitoring and, often, insecticide treatments (Carroll and Hoyt, 1984; Pfeiffer, 1991).

The apple orchard provides a good model for studying the interactions between aphids and their natural enemies. Apple is a perennial woody plant that provides an environment in which natural enemy guilds can evolve into a mature community over numerous generations (Brown, 1999a). Apple trees are also kept vigorous by fertilization, pruning, control of competing vegetation, and often irrigation (Travis, 2000), thus providing a reliable food resource for aphids. Natural enemies of aphids on apple have been well studied in North America (Adams and Prokopy, 1980; Carroll and Hoyt, 1984; Hagley and Allen, 1990; Holdsworth, 1970; Stewart and Walde, 1997; Tracewski et al., 1984). Although populations of *Aphis* spp. on apple have not been well controlled by predators and parasitoids, more

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aphids have been observed on insecticide treated trees than on untreated trees (Holdsworth, 1970; Oatman and Legner, 1961), indicating some biological control. Biological control of apple aphids in Washington State, USA, is adequate only in some years (Carroll and Hoyt, 1984). Biological control of spirea aphid has been more reliable in West Virginia, USA, since the recent arrival of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) (Brown and Miller, 1998). The major predators of *Aphis* spp. on apple have been reported to be *Aphidletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) (Adams and Prokopy, 1980; Brown and Lightner, 1997; Tracewski et al., 1984), chrysopids (Brown and Lightner, 1997; Knowles, 1997), and mirids (Hagley and Allen, 1990). Exclusion cage studies have shown syrphids to be very effective predators of *A. pomi* in Poland (Wnuk, 1977).

This study was conducted to determine if the aphid predator guild on apple in West Virginia, USA, has the potential to control spirea aphids. Specific objectives were to: (1) describe the composition of the predator guild associated with spirea aphid infestations on apple in West Virginia; (2) identify species of predators that are the most effective on apple; (3) determine if the predator guild, and in particular which species in the guild, can control spirea aphid populations on apple; and (4) describe the dynamics of the aphid predator guild in relation to aphid population dynamics.

## 2. Materials and methods

Five separate experiments were conducted to address one or more of the stated objectives in research orchards at the Appalachian Fruit Research Station in Kearneysville, West Virginia, USA, from 1996 to 1998. Data were collected from orchards receiving no insecticides, a reduced insecticide schedule, and a commercially standard insecticide schedule to be representative of all host plant conditions in northeastern North America.

### 2.1. Random sampling

Four apple orchards were sampled in both 1996 and 1997. The first orchard was planted in 1984 and was not treated with insecticides. The second orchard was planted in 1988 and was treated with a reduced insecticide schedule in 1996 and according to commercial standards in 1997 (Virginia Cooperative Extension, 1997). The commercial standard had eight broad-spectrum insecticide applications, mostly organophosphate compounds, from April to August. For the purpose of this study, a reduced insecticide schedule included one broad-spectrum organophosphate application in late April or early May (before aphid colonies appeared) and only *Bacillus thuringiensis* (Bt)

during the time when aphids and their predators were present. The third orchard was planted in 1992 and received a reduced insecticide schedule in 1996 and no insecticides in 1997. The fourth orchard was also planted in 1992 and received a commercial standard insecticide schedule in 1996 and the reduced schedule in 1997. The insecticide treated orchards received horticultural management including fertilization, pruning, and herbicide applications to control vegetation in a 2.5 m wide strip under the trees. The orchard receiving no insecticides also received no horticultural management during the study except for periodic mowing between tree rows and pruning in the winter of 1996 to stimulate shoot growth. In 1996, all four orchards were sampled at an average of 10 day intervals from 20 May to 28 August, with an additional sample on 19 September. In 1997, the average sampling interval was 4.5 days from 27 May to 1 July, with the commercially managed orchard being sampled every 7 days until 21 August due to a longer period of aphid infestation. Sampling in the chemically treated orchards was done at least 5 days after insecticide application for personal safety and to allow time for some equilibration of the aphidophagous guild following treatment.

Sampling consisted of randomly selecting 20 trees in each orchard and randomly, selecting 10 branch terminals per tree. The branch terminal was selected as the sampling unit because it is a discrete unit of habitat with one colony of aphids infesting a single branch terminal. Each terminal selected was examined for the presence of spirea aphids and any predators (including eggs) or parasitoids. If the branch terminal had aphids, the number of infested leaves was recorded as a measure of the size of the aphid population. Data from this random sampling was used to obtain an unbiased estimate of the population density of aphids and predators, pattern of succession of aphid predators, and to detect any density dependent interactions. Data on abundance of each predator was summed over all orchards to analyze guild structure. Correlation analysis was performed to test for relationships between abundance of each predator and aphid abundance at three different scales: individual colonies, mean abundance per tree, and mean abundance per orchard. A *t* test and a  $\chi^2$  test of association ( $2 \times 2$  contingency table) were used to analyze the effect of ants on aphid predator abundance. To compare predator dynamics over time, the aphid infestation was divided into four time periods: colonization phase (through 8 June 1996 and 11 June, 1997), exponential growth phase (9–18 June 1996 and 12–20 June 1997), peak phase (19 June to 3 July 1996 and 21 June to 9 July 1997), and decline phase (beginning 4 July 1996 and 10 July 1997). These stages of aphid infestation are as defined by Smith (1966) but combine his “collapse” and “scarcity” phases into one decline phase.

## 2.2. Sentinel colonies

Potted apple tree seedlings infested from a laboratory colony of spirea aphids were placed near an apple orchard to sample the aphid predator guild at times of the year when natural aphid populations were rare or absent. Eight to 10 trees were placed next to the unsprayed orchard used for random and non-random sampling on 2 May and 24 July 1996, and 28 April, 15 July, and 19 August in 1997. The pots were placed in the soil, leaving the aphid colony about 0.5 m above the ground. Surrounding grass and weeds were cleared away from the potted tree and ants were excluded with Tangle Trap (The Tanglefoot, Grand Rapids, MI) barriers on the trees and support stakes. The colonies were observed daily to count the number of leaves infested with aphids and the presence and abundance of predators and parasitoids. Observations continued until only one infested leaf remained on 75% of the trees. No statistical analysis was done on these data beyond tabulating the occurrence, abundance, and succession of the aphid predator guild.

## 2.3. Non-random sampling

Only the unsprayed and reduced insecticide schedule orchards were sampled in 1996, and in 1997 only the unsprayed orchard planted in 1984 and the reduced spray schedule orchard planted in 1992 were sampled. Thirty-two trees were selected from each orchard in each year. These trees were distributed in 8 clusters of 4 trees, with 4 clusters in the middle of each orchard and one cluster near each edge, with no sample tree closer than 3 trees from the orchard margin. Sampling was conducted at 9-day intervals from 22 May to 17 July in 1996 and at 5-day intervals from 22 May to 30 June in 1997. Newly established spirea aphid colonies, colonies with just a single alate aphid or one alate aphid and a few nymphs on one or two leaves, were marked with plastic flagging at the base of the terminal for subsequent observations. At each sample, new colonies were identified, if any were present, but no more than 10 colonies per tree were observed at any one sample. The same colonies were observed at successive visits until the colony disappeared. When one colony died out, it was replaced with another newly established colony on the same tree for subsequent observations. Data from this non-random sampling were used to evaluate the impact of various predators. A predator was deemed to have impact on the aphid colony if there was a decrease in aphid colony size following the predator's presence in the colony. Three levels of impact were categorized: some impact, when the colony size decreased after the predator was observed, but the colony later increased in size; contributing factor, when

the colony decreased in size after the predator was observed and continued to decline to extinction, although the predator was not present at the final sample for that colony; and causal factor, when the predator was observed in the colony on the last date the colony was observed, or when a predator alone remained on the terminal. Statistical comparisons were made on impact estimates using the normal approximation of binomial data to construct a 95% confidence interval around the impact estimate, using the number of predators per taxa as the sample size (Steel and Torrie, 1960). Confidence intervals were calculated only for taxa with more than 10 individuals.

## 2.4. Laboratory feeding studies

Field collected adult *H. axyridis* were brought into the laboratory for feeding studies to test their potential to eliminate small newly established aphid colonies. After the beetles were starved for 18 h, they were provided with from 1 to 4 aphid colonies in 22 × 22 × 25 cm cages. The cages were left on the laboratory bench for 24 h at 18–22 °C and a 12:12 (L:D)h photophase. Colony size ranged from one aphid to 30 aphids. Trials were conducted with five beetles on 27 May and 28 May, and three beetles on 1 June. Data were recorded on how many colonies were completely eliminated, and how many aphids remained if the colony was not eliminated.

## 2.5. Exclusion studies

Fifty naturally established spirea aphid colonies in the orchard were caged when the colony was newly established (i.e., only one infested leaf with only one alate and <25 aphid nymphs). The cages were 60 cm long by 25 cm in diameter, made of polyester mesh with 22 by 11 thread count per cm (No-see-um mosquito netting, Recreation Equipment, Seattle, WA, USA). A 75 cm long by 1 cm diameter bamboo garden stake was affixed to the branch to provide support for the cage and to allow for unhindered growth of the apple branch in the cage. All predators of any life stage were removed prior to caging and if any predators were observed in the cages during sampling, that branch was deleted from the study (a total of 5 reps were thus deleted). Two similarly sized aphid colonies on the same or adjacent trees were also marked as uncaged controls. Sampling was done at 3–5 day intervals from 18 May to 23 June 1998. Through 9 June, 6–9 new colonies were caged and matching uncaged control colonies identified at each sample. Observations continued until all 150 colonies (50 caged colonies and 100 control colonies) were dead. Data on colony longevity were used to examine the degree of population control provided by the

aphid predator guild. Data analysis was with 95% confidence intervals around the mean for caged and uncaged colonies, analyzed separately for colonies caged prior to 28 May ( $n = 23$ ) and those caged after 28 May ( $n = 22$ ). In the summer of 2002 cages of the same material were placed in the orchard on sample branches to record temperatures inside and outside the cage.

Aphid abundance was also monitored in two orchards, one without insecticides and one with conventional insecticide applications (Virginia Cooperative Extension, 1997) as a chemical predator exclusion experiment. In the insecticide exclusion orchard, additional insecticide applications were made when predators were observed. Applications of methyl parathion, carbaryl, azinphosmethyl, methomyl, and endosulfan were made during the time when aphid colonies were present. All of these pesticides are more toxic to aphid predators than to spirea aphids (Virginia Cooperative Extension, 1997). Nine samples from 15 May to 6 July 1998 were conducted with each sample consisting of 10 randomly selected branch terminals on each of 10 randomly selected trees in each orchard. Differences in aphid abundance between orchards were tested with 95% confidence intervals.

### 3. Results

#### 3.1. Random sampling

From 1996 to 1997, 15,018 apple branch terminals were examined (Table 1), and 6782 aphid colonies were observed. Across the four phases of aphid population development there were about equal numbers of colonies observed during the colonization, exponential growth, and decline phases, and more than twice as many colonies during peak aphid populations. Aphid predator abundance increased from colonization to peak population phase, and declined during the population decline phase. The number of predators per aphid colony, however, almost doubled between the peak and decline phases.

The guild of aphid predators on apple was large and diverse (Table 2), being dominated numerically by the cecidomyiid *A. aphidimyza*. The next most abundant group was lacewings. However, most observations of were of chrysopid eggs of which 52.5% disappeared prior to observation of a larva. Of a total 631 coccinellids observed, 85% were *H. axyridis* (excluding eggs). Syrphids comprised a large portion of the aphid predator guild, but also showed significant loss (42%) from egg to larval stages. Spiders (Araneae) and *Orius insidiosus* (Say) (Hemiptera: Anthocoridae) were also abundant aphid predators (Table 2). Nine other taxa of predators were observed on aphid colonies, including omnivores and predators not commonly associated with aphids (Table 2). Only one of the 6782 colonies observed showed evidence of parasitism, and this had only a few aphid mummies in the colony (none were successfully reared).

Ants (Formicidae) were found in 192 of the 6782 aphid colonies. The predominant species were *Lasius* spp., *Prenolepis* sp., *Formica pallidefulva nitidiventris* Emery, and *F. subsericea* Say. Aphid colonies with ants were significantly larger (4.36 infested leaves per colony) than colonies without ants (2.84 infested leaves per colony) ( $t = 12.19$ ,  $df = 6781$ ,  $P < 0.05$ ). Several of the predators or predator life stages had a significant association ( $P < 0.05$ ) between their abundance and the presence of ants: syrphid larvae ( $X^2 = 14.91$ ), *A. aphidimyza* ( $X^2 = 190.22$ ), lacewing adults ( $X^2 = 4.94$ ), coccinellid larvae ( $X^2 = 5.00$ ), and coccinellid adults ( $X^2 = 16.71$ ). All of these predators were more abundant in aphid colonies that had ants than would have been expected if both predators and ants were distributed randomly.

All the major groups of aphid predators showed some degree of density dependent response to aphid populations. Spiders had an inverse density dependent relationship with aphid abundance (Table 3). *A. aphidimyza* had the strongest correlation with aphid populations at all scales tested, and syrphid larvae, chrysopid larvae, and *O. insidiosus* also had high correlations. Coccinellid larvae were the only group not to have a significant correlation with aphid population density at the orchard level. At the

Table 1

Abundance of spirea aphid and predators by time period from random sampling, 1996 and 1997, Kearneysville, WV

| Population parameter             | Time period |      |      |      | Total             |
|----------------------------------|-------------|------|------|------|-------------------|
|                                  | 1           | 2    | 3    | 4    |                   |
| No. of terminals sampled         | 4400        | 2772 | 3925 | 3921 | 15,018            |
| No. of aphid colonies            | 1271        | 1278 | 2902 | 1331 | 6782              |
| Percentage of terminals infested | 28.9        | 46.1 | 73.9 | 34.0 | 45.2 <sup>a</sup> |
| No. of predators                 | 259         | 628  | 1358 | 1105 | 3350              |
| Predators per colony             | 0.20        | 0.49 | 0.47 | 0.83 | 0.49 <sup>a</sup> |

Time periods correspond with aphid infestation stage: time period 1, aphid colonization; time period 2, rapid growth of aphid population; time period 3, peak aphid population; and time period 4, aphid population decline.

<sup>a</sup> Weighted mean over all time periods.

Table 2

Total aphid predator abundance by time period and by taxonomic group and life stage, based on random sampling, 1996 and 1997, Kearneysville, WV

| Predator                             | Time period |     |     |     | Total |
|--------------------------------------|-------------|-----|-----|-----|-------|
|                                      | 1           | 2   | 3   | 4   |       |
| <i>A. aphidimyza</i>                 | 4           | 254 | 578 | 416 | 1252  |
| Syrphidae, eggs                      | 11          | 61  | 31  | 7   | 110   |
| Syrphidae, larvae                    | 5           | 16  | 39  | 4   | 64    |
| Syrphidae, adults                    | 0           | 3   | 14  | 5   | 22    |
| Chrysopidae, eggs                    | 0           | 52  | 227 | 165 | 444   |
| Chrysopidae, larvae                  | 2           | 16  | 109 | 84  | 211   |
| Chrysopidae, adults                  | 0           | 3   | 9   | 9   | 21    |
| Coccinellidae                        |             |     |     |     |       |
| <i>H. axyridis</i> , larvae          | 81          | 46  | 93  | 85  | 305   |
| <i>H. axyridis</i> , adults          | 31          | 14  | 32  | 20  | 97    |
| <i>C. septempunctata</i> , adults    | 0           | 19  | 20  | 0   | 39    |
| <i>C. maculata</i> , adults          | 0           | 2   | 1   | 0   | 3     |
| <i>Scymnus</i> sp., adults           | 0           | 0   | 7   | 2   | 9     |
| Unidentified larvae                  | 5           | 8   | 0   | 7   | 20    |
| Unidentified eggs                    | 57          | 73  | 1   | 27  | 158   |
| <i>O. insidiosus</i> , all stages    | 1           | 19  | 72  | 141 | 233   |
| Cantharidae, adults                  | 4           | 4   | 6   | 1   | 15    |
| Miridae, all stages                  | 1           | 2   | 41  | 8   | 52    |
| Aranea, all stages                   | 53          | 32  | 59  | 116 | 260   |
| Thysanoptera                         |             |     |     |     |       |
| <i>Leptothrips mali</i> , all stages | 2           | 2   | 4   | 3   | 11    |
| Unidentified, all stages             | 0           | 0   | 0   | 1   | 1     |
| Nabidae, all stages                  | 0           | 1   | 2   | 0   | 3     |
| Gryllidae, all stages                | 1           | 0   | 6   | 4   | 11    |
| Dermaptera, all stages               | 0           | 0   | 5   | 0   | 5     |
| Reduviidae, nymphs                   | 0           | 0   | 1   | 0   | 1     |
| Lampyridae, adults                   | 0           | 0   | 1   | 0   | 1     |
| Cleridae, adult                      | 1           | 0   | 0   | 0   | 1     |
| Parasitoids, aphid mummies           | 0           | 1   | 0   | 0   | 1     |

Time periods correspond with aphid infestation stage: time period 1, aphid colonization; time period 2, rapid growth of aphid population; time period 3, peak aphid population; and time period 4, aphid population decline.

Table 3

Correlations between spirea aphid densities on apple and densities of major predators, correlations reported for three levels of scale comparing the response of predators to aphid population size by orchard, tree, or individual colony

| Predator              | Scale               |                     |                    |
|-----------------------|---------------------|---------------------|--------------------|
|                       | Orchard             | Tree                | Colony             |
| <i>A. aphidimyza</i>  | 0.690 <sup>a</sup>  | 0.434 <sup>a</sup>  | 0.247 <sup>a</sup> |
| Syrphidae eggs        | 0.385 <sup>a</sup>  | 0.169 <sup>a</sup>  | 0.078 <sup>a</sup> |
| Syrphidae larvae      | 0.521 <sup>a</sup>  | 0.203 <sup>a</sup>  | 0.103 <sup>a</sup> |
| Chrysopidae eggs      | 0.376 <sup>a</sup>  | 0.372 <sup>a</sup>  | 0.121 <sup>a</sup> |
| Chrysopidae larvae    | 0.554 <sup>a</sup>  | 0.325 <sup>a</sup>  | 0.094 <sup>a</sup> |
| Coccinellidae larvae  | 0.127               | 0.113 <sup>a</sup>  | 0.056 <sup>a</sup> |
| Coccinellidae adults  | 0.374 <sup>a</sup>  | 0.136 <sup>a</sup>  | 0.051 <sup>a</sup> |
| <i>O. insidiosus</i>  | 0.611 <sup>a</sup>  | 0.329 <sup>a</sup>  | 0.095 <sup>a</sup> |
| Miridae               | 0.345 <sup>a</sup>  | 0.121 <sup>a</sup>  | 0.037              |
| Aranea                | −0.369 <sup>a</sup> | −0.152 <sup>a</sup> | −0.008             |
| All predators, pooled | 0.501 <sup>a</sup>  | 0.462 <sup>a</sup>  | 0.301 <sup>a</sup> |
| Sample size           | 77                  | 1246                | 6782               |

<sup>a</sup> Correlation coefficient significantly different from 0 at  $P < 0.001$ .

colony scale, only the abundance of mirids and spiders were not correlated with aphid abundance. The association between predator abundance and aphid density was strongest for all taxa at the larger (orchard) scale.

### 3.2. Sentinel colonies

The aphid predator guild on the sentinel colonies was strongly dominated by *A. aphidimyza* except for the

Table 4

Percentage composition of the predator guild on 10 large (averaging 15–20 infested larvae per colony) sentinel spirea aphid colonies per trial, 1996–1997

| Predator                        | May 1996 | July 1996 | May 1997 | July 1997 | August 1997 |
|---------------------------------|----------|-----------|----------|-----------|-------------|
| <i>A. aphidimyza</i>            | 77.4     | 92.6      | 0        | 96.8      | 93.2        |
| Coccinellidae                   | 16.6     | 1.1       | 1.6      | 1.9       | 5.3         |
| Syrphidae                       | 4.9      | 3.1       | 98.4     | 1.0       | 0.4         |
| Cantharidae                     | 1.1      | 0         | 0        | 0         | 0           |
| Miridae                         | 0        | 0.5       | 0        | 0         | 0.1         |
| Chrysopidae                     | 0        | 2.0       | 0        | 0.3       | 0.6         |
| <i>O. insidiosus</i>            | 0        | 0.5       | 0        | 0         | 0.2         |
| Carabidae                       | 0        | 0.2       | 0        | 0         | 0           |
| Parasitoids                     | 0        | 0         | 0        | 0         | 0.2         |
| Total no. of predators observed | 283      | 496       | 252      | 1653      | 1627        |

May 1997 sample, which was dominated by syrphids (Table 4). Coccinellids (primarily *H. axyridis* but also including *Cycloneda munda* [Say], *Coccinella septempunctata* L., *Coleomegilla maculata lengi* Timberlake, and *Hippodamia convergens* Guerin) were the only other predator family comprising more than 2% of the guild. A few parasitized mummies were found on one sentinel colony in August 1997. Predator abundance per colony was low early in the year and high late in the season, especially in 1997 (Table 4).

### 3.3. Non-random sampling

The list of predators observed in the non-random sampling portion of this study is presented in Table 5 with estimates of the percentage impact for each

predator. No parasitoids or aphid mummies were observed. The percentage of aphid colonies with each taxon of predator in Table 5 is from the random sampling (Table 2) and is provided to give an unbiased estimate of the relative abundance of each predator. Chrysopid larvae had the largest total impact, 83.5%, and impact as a causal factor, 35.9% (i.e., 83.5% of the 103 chrysopid larvae had an impact on the aphid colony on which they were observed, and 35.9% of these chrysopid larvae were identified as causing the elimination of the colony). Two coccinellid species had 100% impact, but only one individual was observed on a single colony that disappeared and no confidence can be given to their estimate of impact. *A. aphidimyza* had an impact rating significantly less than chrysopid larvae (Table 5), but because of higher abundance,

Table 5

Abundance and impact of aphid predators on spirea aphid populations from non-random sampling of aphid colonies on apple, 1996–1997

| Predator                            | No. observed | % Impact <sup>a</sup> |              |        |         | % Colonies with predator <sup>b</sup> |
|-------------------------------------|--------------|-----------------------|--------------|--------|---------|---------------------------------------|
|                                     |              | Some                  | Contributing | Causal | Total   |                                       |
| <i>A. aphidimyza</i>                | 1277         | 0.9                   | 12.6         | 6.3    | 19.9 d  | 5.6 a                                 |
| Syrphid egg and adult               | 94           | 1.1                   | 0.0          | 0.0    | 1.1 f   | 1.3 e                                 |
| Syrphid larvae                      | 36           | 2.8                   | 19.4         | 13.9   | 36.1 c  | 0.8 f                                 |
| Chrysopid egg and adult             | 312          | 1.3                   | 1.9          | 0.6    | 3.8 e   | 5.8 a                                 |
| Chrysopid larvae                    | 103          | 5.8                   | 41.7         | 35.9   | 83.5 a  | 2.8 d                                 |
| <i>H. axyridis</i> larvae and adult | 219          | 2.3                   | 16.9         | 18.7   | 37.9 c  | 4.1 b                                 |
| <i>C. septempunctata</i> adult      | 36           | 8.3                   | 50.0         | 5.6    | 63.9 b  | 0.6 g                                 |
| <i>C. maculata</i> adult            | 1            | 100.0                 | 0.0          | 0.0    | 100.0   | <0.1 i                                |
| <i>Anatis labiculata</i> adult      | 1            | 0.0                   | 100.0        | 0.0    | 100.0   | 0.0 i                                 |
| Cantharid adult                     | 6            | 33.3                  | 16.7         | 0.0    | 50.0    | 0.2 h                                 |
| <i>O. insidiosus</i>                | 76           | 1.3                   | 23.7         | 17.1   | 42.1 bc | 3.3 c                                 |
| Mirid                               | 31           | 3.2                   | 38.7         | 3.2    | 45.2 b  | 0.7 fg                                |
| Aranea                              | 62           | 1.6                   | 1.6          | 0.0    | 3.2 ef  | 3.8 bc                                |
| <i>L. mali</i>                      | 9            | 0.0                   | 11.1         | 0.0    | 11.1    | 0.2 h                                 |

<sup>a</sup> Impact defined as: some, when the colony size decreased after the predator was observed, but the colony later increased in size; contributing, when the colony decreased in size after the predator was observed and continued to decrease until there were no more aphids present; and causal, when the predator was observed in the colony at the last time the colony was observed. Total impact by predator followed by the same letter are not significantly different based on normal approximation of binomial data with 95% confidence intervals using abundance of that predator as the sample size (confidence intervals calculated only for taxa with >10 individuals).

<sup>b</sup> Percentage of colonies containing each predator taxon is from data collected in random sampling in the same orchards over the same time period. Percentages followed by the same letter are not significantly different based on normal approximation of binomial data with 95% confidence intervals using number of colonies sampled (6782) as the sample size.

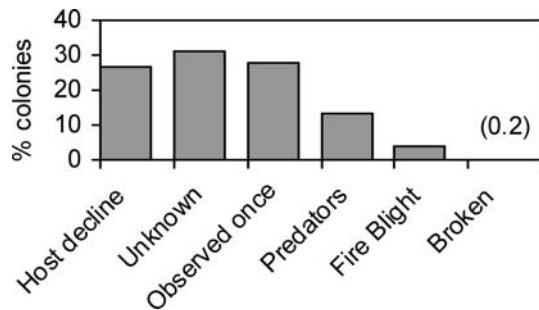


Fig. 1. Observed cause of spirea aphid colony disappearance for the 1253 colonies sampled in the non-random sampling, 1996 and 1997; “host decline” are colonies that died out when the branch terminal stopped growing and “observed once” indicates colonies that disappeared without an observable cause after only one observation.

*A. aphidimyza* would have affected more colonies. *C. septempunctata* adults had a significantly higher impact rating than *H. axyridis*, but because of the greater abundance of *H. axyridis*, the latter species would have had a greater effect on aphid populations. Syrphid eggs and adults and chrysopid eggs are included because of their potential impact on aphid colonies, even when larvae were not observed. Combining the impact ratings with the abundance of each predator, *A. aphidimyza*, chrysopid larvae, and *H. axyridis* had the greatest regulating effect on spirea aphid populations (Table 5).

Overall, 1253 colonies were observed during the non-random sampling. The causes of the final disappearance of these colonies are shown in Fig. 1. Predators were credited, through direct observation, with causing the elimination of 14.4% of the colonies. The largest identified cause of colony extinction was the cessation of branch growth (29.1% of colonies, labeled “host decline” Fig. 1) such that it was no longer a suitable host for spirea aphids. Colonies disappeared with no apparent cause 30.8% of the time, and an additional 21.7% of the colonies also disappeared with no apparent cause after being observed only once when the colony was young. Fire blight (disease caused by the bacterium *Erwinia amylovora*) and broken branches caused the destruction of 4.4 and 0.2% of aphid colonies, respectively (Fig. 1).

### 3.4. Laboratory feeding study

This study was done to provide data to help interpret the disappearance of those young aphid colonies in the non-random study that were only observed once. Adult *H. axyridis* completely destroyed 77% of the 26 small aphid colonies provided in the laboratory in 24 h. A total of 95% of the 195 aphids were eaten. Only first instar aphids located between the leaf axils of expanding leaves and the stem escaped predation.

### 3.5. Exclusion study

There were 23 spirea aphid colonies caged to exclude predators prior to 28 May with 54 uncaged colonies as controls, and 22 aphid colonies caged after 28 May with 46 uncaged controls. Caged aphid colonies survived significantly longer than uncaged colonies during both time periods (confidence intervals,  $P < 0.05$ ) (Fig. 2). The difference in colony longevity between caged and uncaged colonies was smaller late in the season than earlier (Fig. 2). Both caged and uncaged terminals remained active and suitable for aphid colonization and development for the duration of the study. In the summer of 2002, cages of the same material showed that there was no difference in temperature in the cage and on a branch outside the cage in the shade. In direct sunlight the cage was 1 °C warmer than an uncaged branch. In the exclusion studies the caged branches were in the shade for most of the day.

In the insecticide-treated orchard only a few adult coccinellids, syrphid eggs, and chrysopid eggs were observed, whereas predators were common in the unsprayed orchard. The insecticide-treated orchard had significantly larger spirea aphid colonies than in the

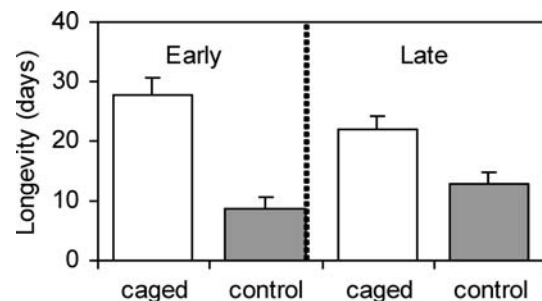


Fig. 2. Mean colony longevity ( $\pm 95\%$  confidence interval) for 23 caged and 54 uncaged spirea aphid colonies first sampled prior to 28 May and 22 caged and 46 uncaged colonies first sampled after 28 May.

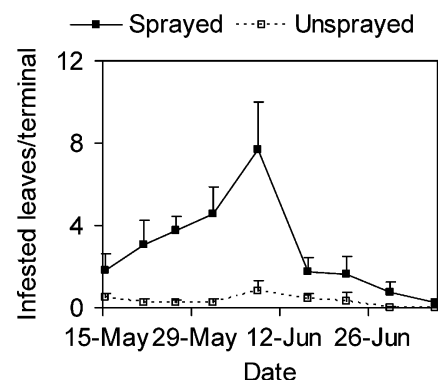


Fig. 3. Mean spirea aphid population size, infested leaves/terminal averaged over all terminals sampled ( $\pm 95\%$  confidence interval) in insecticide treated (solid line) and untreated (dotted line) orchards.

unsprayed orchard at all sample dates except 6 July (confidence intervals,  $P < 0.05$ ) (Fig. 3). The variable, infested leaves/terminal (Fig. 3), incorporates both size of aphid colony and number of colonies by averaging the number of infested leaves per terminal over all branch terminals examined.

#### 4. Discussion

A portion of the data from this study have been used previously to compare the synchrony of various predator populations with spirea aphid populations and to estimate effects of different levels of insecticide use (Brown, 1999b). *H. axyridis* was the only predator to be abundant prior to peak aphid population density (Table 2; Brown, 1999b). *A. aphidimyza*, *O. insidiosus*, chrysopids, *H. axyridis*, and mirids all peaked in abundance during the peak in aphid abundance (Brown, 1999b). Spider abundance was high throughout the period of aphid population increase, but peaked only after aphid populations began to decline. Aphid predators have been generally considered to be ineffective in controlling aphid populations because of their inability to respond rapidly enough to aphid population growth (Frazer, 1988). Results from the current study largely support this general conclusion (Tables 2 and 5; Fig. 1), however, the abundance of adult and larval *H. axyridis* during the initial stages of aphid infestation (Table 2) indicate a potential for this predator to negatively impact aphid population growth.

There was a surprisingly small effect of insecticide use on the abundance of aphid predators (Brown, 1999b). Only coccinellids and spiders were significantly more abundant in reduced pesticide orchards. Chrysopids and *O. insidiosus* were more abundant in orchards receiving standard insecticide applications, likely in response to a greater abundance of mite prey in these orchards. Similar results were found by Brown and Lightner (1997) sampling the same guild prior to the appearance of *H. axyridis* in West Virginia orchards. Both studies, however, sampled approximately a week or more after insecticide application, allowing ample time for recolonization of the orchard by predators.

The total number of predators per colony was highest during aphid population decline and lowest during aphid colonization (Table 1). However, the aphidophagous guild is large and diverse (Table 2), so it is possible that individual species could play roles in population control that may be masked by examining total guild dynamics. For example, *H. axyridis* was the most abundant predator during the aphid colonization stage (Table 2) when the expected effect of predation on aphid populations would be greatest (Smith, 1966). Both abundance and impact of syrphid and chrysopid larvae may have been underestimated due to their habits of

nocturnal feeding and resting outside the aphid colony during daylight hours (Brown and Schmitt, 2001; Rotheray, 1989) when sampling took place. However, chrysopids and syrphids both suffered high mortality between the egg and larval stages, perhaps due to intraguild predation (Lucas et al., 1998), thus reducing their overall effect on spirea aphid populations. Since *A. aphidimyza* became abundant only during and after peak aphid population density, this species may not be as useful in preventing aphid outbreaks, as it is in decreasing peak aphid densities. It is of note that in the apple ecosystem, ants did not interfere with aphid predations as has been documented in other systems (Way, 1963). Parasitoids were not abundant enough in any samples to exert any degree of aphid population control.

All the abundant groups of predators showed some degree of density dependence on aphid population abundance (Table 3). *A. aphidimyza*, *O. insidiosus*, syrphid larvae, and chrysopid larvae were particularly responsive to increases in aphid density, with correlations  $>0.5$  at the orchard scale (Table 3). Stewart and Walde (1997) also found that *A. aphidimyza* showed a strong density dependent response toward aphids (*A. pomi*) on apple. Coccinellids had a surprisingly low level of density dependence with spirea aphid, with no significant correlation between coccinellid larvae and aphid density at the orchard scale. A weak response of individual coccinellids to aphid density was also found by Ives et al. (1993), but they found an overall population level aggregation to high aphid density. A propensity for cannibalism among coccinellids (Yasuda and Shinya, 1997) and the availability of alternative prey also reduces their apparent density dependence on aphid populations. All predators had a higher correlation with aphid density at the orchard scale than at the smaller tree or individual colony scale (Table 3). The predator populations observed in this study seemed to react more toward area-wide aphid densities than to aphid population changes on individual trees or single colonies. Spiders had a significantly negative correlation with aphid density (Table 3), indicating they would not be effective at regulating aphid populations. Most of the spiders observed were hunting or crab spiders which may be deterred from foraging on branches infested with aphids due to the accumulation of honeydew and aphid bodies. Wyss et al. (1995) found that web-building spiders were important predators of *Dysaphis plantaginea* (Passerini) (Homoptera: Aphididae) on apple, but only in the fall when alate aphids were returning to apple to deposit overwintering eggs.

Sentinel colonies were used to sample the aphidophaga guild at times of the year when spirea aphids generally are not abundant on apple. *A. aphidimyza*, coccinellids, and syrphids comprised more than 95% of the predators colonizing sentinel colonies (Table 4).



Later in the summer, July 1996 and August 1997, there was a larger diversity of predators in aphid colonies. There was a noticeable absence of *A. aphidimyza* in May 1997, the earliest sample conducted. Early season absence may inhibit the ability of this otherwise abundant predator to control spirea aphid on apple and could explain the delayed synchrony of *A. aphidimyza* with aphid population growth (Brown, 1999b). Reports of control of apple aphid populations by *A. aphidimyza* have been from more northern climates of North America (Adams and Prokopy, 1980; Stewart and Walde, 1997) where the predator and prey may be better synchronized. Parasitism in the sentinel colonies was rare and occurred only in the last sample of the year. Although these sentinel colonies were on small trees outside orchards, they showed that these predators were capable of responding to spirea aphid populations at all times of the growing season.

The exclusion cages had a minimal effect on the microclimate of the enclosed branches, and branch growth continued throughout the duration of the exclusion study. Host plant differences can also be ruled out as an explanation of differences in aphid colony longevity, because both caged and uncaged colonies were on the same trees. Spirea aphids on apple become agitated in the presence of predators, but do not drop from the branches and rarely migrate except as alates (personal observation), and alate aphids were not observed except on the oldest colonies in the caged treatment. Thus, differences in emigration cannot explain differences in colony longevity (Fig. 2). Results from the two exclusion studies, therefore, give a strong indication that natural enemies can impose some degree of regulation in natural spirea aphid populations on apple. The caged exclusion experiment also showed more predator pressure early in the study than later (Fig. 2) at the time when *H. axyridis* was the only abundant predator (Table 2).

The predator impact data presented in Table 5, and the overall effect of predation in Fig. 1 should be considered as a minimum estimate of the importance of predation on aphid population dynamics. The data were generated from observations made at 5–9 day intervals, thus allowing opportunity for many predators, especially mobile adults, to visit colonies and depart without leaving a sign of their presence. Although only 14.4% of the aphid colonies were identified as being eliminated by predators, an additional 27.5% of the colonies did have evidence of some predator impact. No apparent cause of colony death was attributed to 52.5% of all colonies observed. It is likely that some of these colonies were eliminated by predator activity that was undetected. Host decline was responsible for 29.1% of the colonies' demise, representing the number of colonies that did not survive due to declining host suitability.

In particular, the impact of adult *H. axyridis* could also have been underestimated because of their mobility and voracity. Many of the small, newly established colonies (21.7%) disappeared after only one observation (Fig. 1). These colonies could easily have been destroyed by voracious, highly mobile predators. Only *H. axyridis* adults possess these attributes, and were abundant enough early in aphid population development, to eliminate a large number of colonies. The laboratory feeding trials indicate that *H. axyridis* adults are capable of eliminating up to 4 colonies in 24 h.

Considering the data on predator synchrony with spirea aphid populations on apple (Brown, 1999b), overall predator abundance and impact, and results of the exclusion trials, *H. axyridis* appears to be the most important predator of spirea aphid on apple in West Virginia. Other predators such as *A. aphidimyza*, chrysopids, syrphids, and *O. insidiosus* contribute to aphid predation, but only *H. axyridis* appears capable of significant impact during the critical initial stages of population increase. In a similar study conducted on citrus, coccinellids, including *H. axyridis*, were also found to be the most important predators of the brown citrus aphid, *Toxoptera citricida*, in Florida and Puerto Rico (Michaud, 1999). In the spirea aphid–apple system, the important interaction appears to be a response of adult *H. axyridis* to young aphid colonies during the colonization phase of population growth. The actual impact of *H. axyridis* adults on spirea aphid population dynamics warrants further quantification in controlled laboratory and field experiments.

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## References

- Adams, R.G., Prokopy, R.J., 1980. *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae): an effective predator of the apple aphid (Homoptera: Aphididae) in Massachusetts. *Protection Ecology* 2, 27–39.
- Blackman, R.L., Eastop, V.F., 1984. *Aphids on the World's Crops: An Identification Guide*. Wiley, New York.
- Brown, M.W., 1999a. Applying principles of community ecology to pest management in orchards. *Agriculture, Ecosystems and Environment* 73, 103–106.
- Brown, M.W., 1999b. Temporal changes in the aphid predator guild in eastern North America. *Proc. integrated plant protection in orchards. IOBC wprs Bull.* 23, 7–11.
- Brown, M.W., Hogmire, H.W., Schmitt, J.J., 1995. Competitive displacement of apple aphid by spirea aphid (Homoptera:

- Aphididae) on apple as mediated by human activities. *Environmental Entomology* 24, 1581–1591.
- Brown, M.W., Lightner, G.W., 1997. Recommendations on minimum experimental plot size and succession of aphidophaga in West Virginia, USA, apple orchards. *Entomophaga* 42, 257–267.
- Brown, M.W., Miller, S.S., 1998. Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. *Entomological News* 102, 136–142.
- Brown, M.W., Schmitt, J.J., 2001. Seasonal and diurnal dynamics of beneficial insect populations in apple orchards under different management intensity. *Environmental Entomology* 30, 415–424.
- Carroll, D.P., Hoyt, S.C., 1984. Natural enemies and their effects on apple aphid, *Aphis pomi* DeGeer (Homoptera: Aphididae), colonies on young apple trees in central Washington. *Environmental Entomology* 13, 469–481.
- Frazer, B.D., 1988. Predators. In: Minks, A.K., Harrewijn, P. (Eds.), *Aphids: Their Biology, Natural Enemies and Control*, vol. B. Elsevier, New York, pp. 217–230.
- Hagley, E.A.C., Allen, W.R., 1990. The green apple aphid, *Aphis pomi* DeGeer (Homoptera: Aphididae), as prey of polyphagous arthropod predators in Ontario. *Canadian Entomologist* 122, 1221–1228.
- Hamilton, G.C., Swift, F.C., Marini, R., 1986. Effect of *Aphis pomi* (Homoptera: Aphididae) density on apples. *Journal of Economic Entomology* 79, 471–478.
- Holdsworth, R.P., 1970. Aphids and aphid enemies; effect of integrated control in an Ohio apple orchard. *Journal of Economic Entomology* 63, 530–535.
- Ives, A.R., Kareiva, P., Perry, R., 1993. Response of a predator to variation in prey density at three hierarchical scales: lady beetles feeding on aphids. *Ecology* 74, 1929–1938.
- Kaakeh, W., Pfeiffer, D.G., Marini, R.P., 1992. Combined effects of spirea aphid (Homoptera: Aphididae) and nitrogen fertilization on net photosynthesis, total chlorophyll content, and greenness of apple leaves. *Journal of Economic Entomology* 85, 939–946.
- Kaakeh, W., Pfeiffer, D.G., Marini, R.P., 1993. Effect of *Aphis spiraeicola* and *A. pomi* (Homoptera: Aphididae) on the growth of young apple trees. *Crop Protection* 12, 141–147.
- Knowles, K.L., 1997. Impact of low-spray mating disruption programs on aphidophagous insect populations in Virginia apple orchards. M.S. Thesis, Virginia Polytechnic Institute and State University, Blacksburg, VA.
- Lucas, E., Codere, D., Brodeur, J., 1998. Intraguild predation among aphid predators: characterization and influence of extraguild prey density. *Ecology* 79, 1084–1092.
- Michaud, J.P., 1999. Sources of mortality in colonies of brown citrus aphid, *Toxoptera citricida*. *BioControl* 44, 347–367.
- Oatman, E.R., Legner, E.F., 1961. Bionomics of the apple aphid, *Aphis pomi*, on young nonbearing apple trees. *Journal of Economic Entomology* 54, 1034–1037.
- Pfeiffer, D., 1991. Biology and management of aphids on apple. In: Williams, K. (Ed.), *New Directions in Tree Fruit Pest Management*. Good Fruit Grower, Yakima, Washington, pp. 169–183.
- Pfeiffer, D.G., Brown, M.W., Varn, M.W., 1989. Incidence of spirea aphid (Homoptera: Aphididae) in apple orchards in Virginia, West Virginia, and Maryland. *Journal of Entomological Science* 24, 145–149.
- Rotheray, G.E., 1989. Aphid Predators. *Naturalists' Handbooks* 11. Richmond Publishing, Slough, England.
- Smith, R.F., 1966. Summing-up of the section V. In: Hodek, I. (Ed.), *Ecology of Aphidophagous Insects*. Academia, Prague and Dr W. Junk, The Hague, pp. 285–287.
- Steel, R.G.D., Torrie, J.H., 1960. *Principles and Procedures of Statistics*. McGraw-Hill, New York.
- Stewart, H.C., Walde, S.J., 1997. The dynamics of *Aphis pomi* De Geer (Homoptera: Aphididae) and its predator, *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae), on apple in Nova Scotia. *Canadian Entomologist* 129, 627–636.
- Tracewski, K.T., Johnson, P.C., Eaton, A.T., 1984. Relative densities of predaceous Diptera (Cecidomyiidae, Chamaemyiidae, Syrphidae) and their aphid prey in New Hampshire, USA, apple orchards. *Protection Ecology* 6, 199–207.
- Travis, J.W. (Ed.), 2000. *Pennsylvania Tree Fruit Production Guide 2000–2001*. The Pennsylvania State University, University Park, PA.
- Virginia Cooperative Extension, 1997. 1997 Spray bulletin for commercial tree fruit growers. Publication 456-419. Blacksburg, Virginia.
- Yasuda, H., Shinya, K., 1997. Cannibalism and interspecific predation in two ladybirds in relation to prey abundance in the field. *Entomophaga* 42, 153–163.
- Wnuk, A., 1977. The natural enemy *Episyrphus balteatus* (Deg.) (Diptera: Syrphidae) limiting *Aphis pomi* Deg. (Homoptera: Aphididae). *Polskie Pismo Entomologiczne* 47, 455–460 (English summary).
- Wyss, E., Niggli, U., Nentwig, W., 1995. The impact of spiders on aphid populations in a strip-managed apple orchard. *Journal of Applied Entomology* 119, 473–478.
- Way, M.J., 1963. Mutualism between ants and honeydew-producing Homoptera. *Annual Review Entomology* 8, 307–344.